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Cranial Circulation and Relationships of the Colugo *Cynocephalus* (Dermoptera, Mammalia)

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ABSTRACT

The superordinal relationships of the extant colugo *Cynocephalus* currently are the subject of controversy, with conflicting hypotheses derived from skeletal, neuroanatomical, and biochemical analyses. To evaluate these hypotheses, the cranial circulation was investigated in serially sectioned prenatal and juvenile colugos. The cranial vascular pattern and associated osseous features have played a crucial role in assessing higher-level relationships among mammals and heretofore have not been described in detail for the colugo.

Cynocephalus exhibits one of the most highly derived cranial vascular patterns among eutherians. The internal carotid and stapedial arteries are lacking, with their terminal branches annexed to the cerebral circulation and external carotid. Situated in the back of the orbit and extending intracranially into the cavernous sinus is a rete mirabile that is connected with the external carotid system via multiple channels (intra- and extracranial). As important conduits for the dural sinuses, there are a well-developed sinus communicans and vena diploëtica magna; a postglenoid vein and foramen are wholly absent.

Derived features of the cranial circulation are shared between the colugo and a variety of eutherian groups (e.g., bats, euprimates, lagomorphs, artiodactyls) and by themselves support several different placements for Dermoptera. On a more definitive note, no convincing derived features of the cranial circulation were identified allying colugos with early Tertiary plagiomenids or archaic primates.

INTRODUCTION

The phylogenetic relationships of the colugos or "flying lemurs," specialized gliders from southeast Asia, have long puzzled mammalian systematists. Because the single living genus *Cynocephalus* is so distinctive, most authors agree that it be allocated its own order, Dermoptera (Gregory, 1910; Simpson, 1945; but see Van Valen, 1967). However,

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the identity of the extinct members and the higher-level affinities of Dermoptera are highly controversial.

The first unequivocal fossil dermopteran, *Dermotherium major* from the late Eocene of Thailand, a left lower jaw with two molars, has only recently been reported (Ducrocq et al., 1992). Just a handful of other extinct taxa has been assigned to Dermoptera, but opinions on these allocations vary dramatically. Because the early Tertiary plagiomenids have dental resemblances to colugos, they have been widely regarded as dermopterans (Matthew, 1918; Rose and Simons, 1977). However, newly uncovered basicranial remains of plagiomenids show affinities not with colugos, but with elephant shrews, desman moles, and (to a lesser extent) euprimates, from which MacPhee et al. (1989) conclude that Plagiomenidae is best regarded as Eutheria incertae sedis. Some archaic primates have been identified as dermopterans by Beard (1990), who argued that early Tertiary paromomyids may have had a patagium (flight membrane) because their intermediate phalanges are longer than the proximal ones, as occurs in colugos. However, Krause (1991) raised serious concerns about Beard's identifications and associations of these disarticulated digital elements.

Several conflicting hypotheses currently account for the superordinal relationships of Dermoptera. Some authors (e.g., Novacek and Wyss, 1986; Wible and Novacek, 1988; Baker et al., 1991) unite colugos with bats (chiropterans) within the superorder Archonta, which also includes tree shrews (scandentians), euprimates, and archaic primates (plesiadapids and paromomyids) (fig. 1A). Among the characters supporting a colugo + bat clade is a patagium continuously attached between the digits of the manus. Other authors (e.g., Pettigrew et al., 1989; Pettigrew, 1991a, 1991b) link colugos with Old World fruit bats (megachiropterans) and euprimates, chiefly because of shared resemblances in the central nervous system; the echolocating bats (microchiropterans) lack these neural characters and are excluded from this grouping (fig. 1B). Under the latter hypothesis, mega- and microchiropterans have independently acquired wings for powered flight. Lastly, several recent studies of DNA sequences (e.g., Adkins and Honeycutt, 1991; Bailey et al., 1992; Ammerman and Hillis, 1992) have supported bat monophyly, but not a monophyletic Archonta; colugos are allied closer to euprimates and tree shrews than to bats (fig. 1C, D).

Resolution of these controversies awaits the discovery of relevant extinct taxa and the collection of additional anatomical, behavioral, and biochemical data from the living forms. Of particular interest among the living taxa is the colugo, because it has not been as intensively studied as have euprimates, bats, or tree shrews with regard to many features. A prime example is the cranial circulation. The pattern of arterial blood supply to the head is well known for euprimates (MacPhee and Cartmill, 1986), bats (Tandler, 1899; Grosser, 1901), and tree shrews (Cartmill and MacPhee, 1980), but is poorly known for colugos. Additionally, the cranial circulation is relevant to the controversies mentioned above, because it has proven an important source of characters for phylogenetic analysis at the superordinal level among eutherians (Wible, 1986, 1987). The purpose of this report is to provide new anatomical data for evaluating the relationships of the colugo, by describing its cranial circulation and comparing it to that of other mammals.

ACKNOWLEDGMENTS

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ABBREVIATIONS

Institutional

AMNH	Department of Mammalogy, American Museum of Natural History
DUCEC	Duke University Comparative Embryological Collection

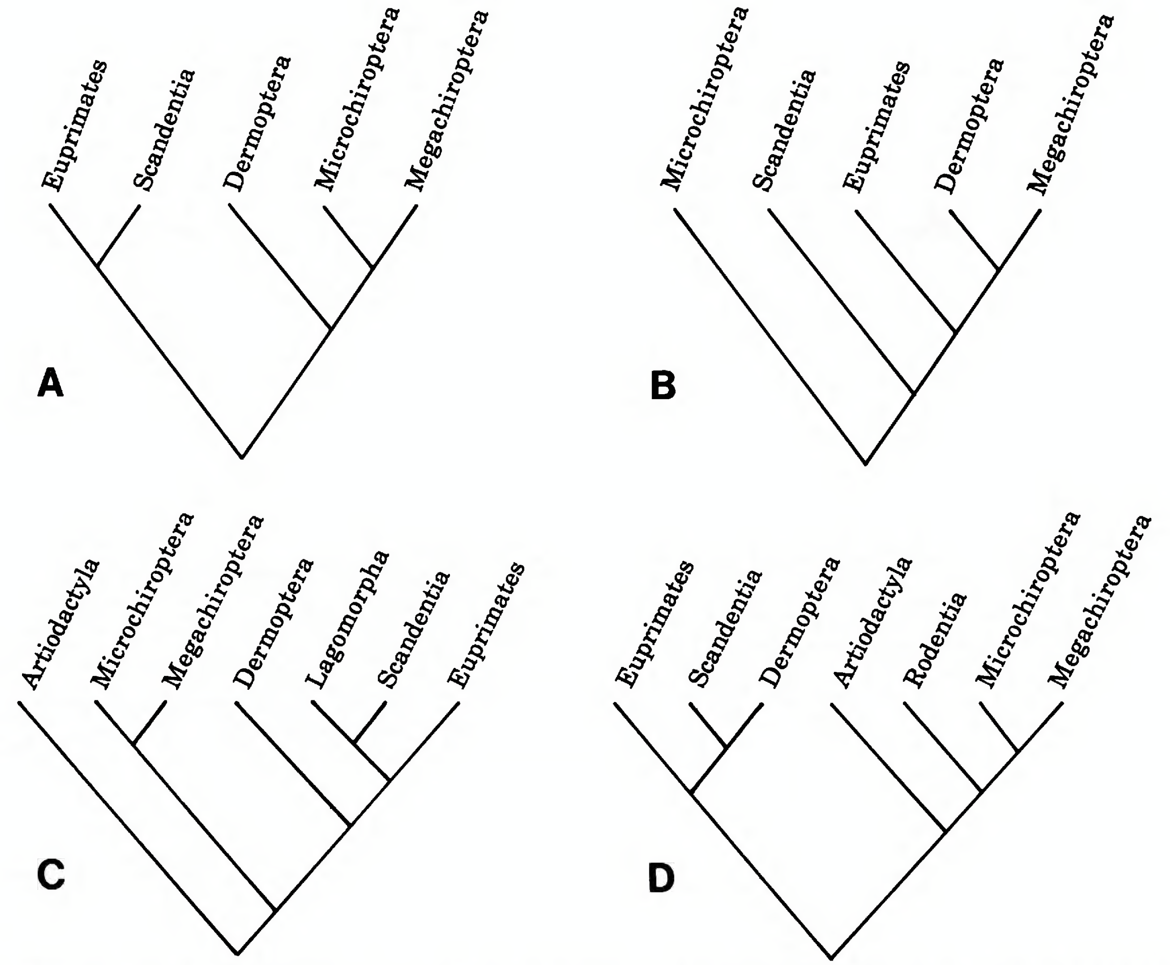

Fig. 1. Hypotheses of superordinal relationships of colugos. **A**, Superorder Archonta, following Wible and Novacek (1988). **B**, Chiropteran diphyly, following Pettigrew et al. (1989). **C**, Most parsimonious tree from Bailey et al. (1992). **D**, One of three hypotheses from Adkins and Honeycutt (1991), substituting higher-level taxa for genera and omitting the outgroup, the xenarthran *Dasypus*.

FMNH	Division of Mammals, Field Museum of Natural History
USNM	Division of Zoology, United States National Museum

Anatomical

aa	arteria anastomotica
ab	auricular branch of vagus
ac	aqueductus cochleae
adm	arteria diploëtica magna
ap	ascending pharyngeal a.
as	alisphenoid
at	anterior tympanic a.
av	vestibular aqueduct
ba	basilar a.
bf	anterior and posterior basicapsular fissures
bo	basioccipital
bs	basisphenoid
bu	buccal a.
ca	anterior cerebral a.
cat	cartilage of the auditory tube
"cat"	fused cartilage of auditory tube and entotympanics
cb	cervical branch
cc	cochlear capsule
cca	common carotid a.
cev	capsuloparietal emissary v.
cf	carotid foramen
ci	ciliary a.
cm	middle cerebral a.
cmb	communicating branches between maxillary and pterygoorbital aa.
cof	cranio-orbital foramen
cop	commissura orbitoparietalis
cos	cranio-orbital sinus

cp	posterior cerebral a.
cs	cavernous sinus
ct	chorda tympani nerve
dt	deep temporal a.
e	ectotympanic
ec	external carotid a.
edv	v. with endolymphatic duct
ee	external ethmoid a.
ef	ethmoid foramen
ejv	external jugular v.
eo	exoccipital
eS	element of Spence
ew	epitympanic wing
fa	facial a.
fc	fenestra cochleae (round window)
fm	foramen magnum
fo	foramen ovale
fr	frontal
fro	frontal a.
fv	fenestra vestibuli (oval window)
g	gonial
gf	glenoid fossa
gp	greater petrosal nerve
hf	hypoglossal foramen
ia	inferior alveolar a.
iam	internal acoustic meatus
ib	intracranial branch
ic	internal carotid a.
icn	internal carotid nerve
ijv	internal jugular v.
io	infraorbital a.
ip	a. with inferior petrosal sinus
ips	inferior petrosal sinus
IX	glossopharyngeal nerve
jf	jugular foramen
ju	jugal
la	lacrimal a.
lb	laryngeal branch
ld	lateral division of external carotid a.
li	lingual a.
lp	lesser petrosal nerve
lpa	lamina parietalis
lsc	prominence of lateral semicircular canal
m	malleus
ma	meningeal a.
mb	muscular branches
Mc	Meckel's cartilage
md	medial division of external carotid a.
me	mastoid eminence
mev	mastoid emissary v.
mf	mastoid foramen
mv	meningeal v.
mx	maxillary a.
oa	occipital a.
oc	occipital condyle
of	optic foramen
og	otic ganglion
or	orbital rete
os	orbitosphenoid
ov	occipital v.
pa	posterior auricular a.
pal	ascending palatine a.
par	parietal
pc	pars canalicularis of auditory capsule
pca	posterior communicating a.
pdv	v. with perilymphatic duct
pe	petrosal
pf	piriform fenestra
pfc	prefacial commissure
pff	primary facial foramen
pgf	postglenoid foramen
pgp	postglenoid process
pgv	postglenoid v.
phv	pharyngeal v.
pm	posterior meningeal a.
pmv	posterior meningeal v.
po	pterygoorbital a.
pov	pterygoorbital v.
pp	pharyngeal plexus
pr	promontorium of petrosal
pt	pterygoid
ptc	posttemporal canal
Rc	Reichert's cartilage
ri	ramus inferior of stapedial a.
rio	ramus infraorbitalis
rm	ramus mandibularis
rp	ramus posterior of stapedial a.
rs	ramus superior of stapedial a.
rso	ramus supraorbitalis
rt	ramus temporalis
sa	stapedial a.
saf	subarcuate fossa
sc	sinus communicans
scg	superior cervical ganglion
sf	stapedius fossa
sm	stylomastoid a.
sps	superior petrosal sinus
sq	squamosal
ss	sigmoid sinus
st	superficial temporal a.
stf	squamotympanic fissure
tf	transverse facial a.
thy	superior thyroid a.
tn	tympanic nerve
ts	transverse sinus
tt	tegmen tympani
va	vertebral a.
vld	v. with lateral division of external carotid a.
vdm	vena diploëtica magna
vmd	v. with medial division of external carotid a.
vv	vertebral v.
$V_{1,2}$	opening for ophthalmic and maxillary divisions of trigeminal nerve

V_3	mandibular division of trigeminal nerve (or its opening)
VII	facial nerve
X	vagus nerve

MATERIALS AND METHODS

Cranial vessels were studied in the serially sectioned specimens of *Cynocephalus* listed below by increasing size. All specimens are housed in the Duke University Comparative Embryological Collection, Durham, North Carolina. The ontogeny of the tympanic floor and roof has been described separately for these specimens by Wible and Martin (1993).

(1) *Cynocephalus variegatus,* DUCEC 804. Head was embedded in paraffin and sectioned in a frontal plane at 15 μm. Stain: Mallory's trichrome. Crown-rump length (CRL): 88 mm. Head length (HL): 28 mm.

(2) *Cynocephalus* sp., DUCEC 8310. As above, but CRL: 107 mm.

(3) *Cynocephalus variegatus,* DUCEC 806. As above, but right half of head sectioned in a sagittal plane at 20 μm and left half in a frontal plane at 15 and 20 μm. Stain: Azan. CRL: 136 mm. HL: 44 mm.

(4) *Cynocephalus* sp., DUCEC 839. As above, but whole head sectioned in a frontal plane at 20 and 40 μm. Stain: Azan. CRL: 150 mm. HL: 49 mm.

The species identification of Specimens 1 and 3 is suspect. Two species of *Cynocephalus* are generally recognized (e.g., Nowak, 1991)—*C. volans* (southern Philippines) and *C. variegatus* (southern parts of Thailand and Indochina, Malay Peninsula, Sumatra, Java, Borneo, and many nearby islands). Though listed as *C. variegatus* in the DUCEC catalog, Specimens 1 and 3 may be *C. volans* because they are said to be from the Philippines. Locality information for Specimens 2 and 4 was not available.

Information regarding the age of the specimens was also not available. Specimens 1 and 2 are surely prenatal, given the prevalence of cartilage in their chondrocrania (figs. 3A, 4B, 5A). Specimens 3 and 4 may be neonates or even juveniles, given that their chondrocrania are largely ossified (fig. 6A) and that the state of development of their auditory bullae resembles that of a juvenile *C. variegatus* (USNM 307553). Whereas the tympanic floor includes only a ring-shaped ectotympanic and a simple cartilage of the auditory tube in Specimens 1 and 2 (fig. 3B), there is a complete auditory bulla in Specimens 3 and 4, composed of the expanded ectotympanic and a fused cartilage of the auditory tube and entotympanics (fig. 6B; Wible and Martin, 1993). Specimens 3 and 4 are referred to as juveniles in the text.

The following descriptions and illustrations were derived primarily from Specimen 2, DUCEC 8310, with significant variations noted in the text. The illustrations in figures 3–6 were redrawn from computer-generated reconstructions made with a three-dimensional reconstruction program from Jandel Scientific, Sausalito, California (PC3D, version 5.0). Every fifth section for DUCEC 8310 (figs. 3–5) and every tenth for DUCEC 806 (fig. 6) were projected and drawn. After aligning the sections, the outlines of relevant structures were traced with a Jandel digitizing tablet. The PC3D program, running on an IBM PS2, stacked the outlines from each section to produce a three-dimensional representation that could be viewed in any specified orientation.

Vessels were not studied in adult *Cynocephalus*. Nevertheless, given that all specimens exhibited essentially the same pattern and given that the largest specimens may be neonates or juveniles, it seems likely that the vascular pattern described below is repeated in the adult. Osseous features associated with the cranial vasculature in the sectioned specimens were checked in adult skulls of *C. volans* and *C. variegatus* in the Department of Mammalogy, American Museum of Natural History.

DESCRIPTIONS

ARTERIES

A diagrammatic representation of the major cranial arteries in *Cynocephalus* sp. (DUCEC 8310) is shown in figure 2. The most striking feature is the orbital rete, a complicated network of intertwined arteries situated at the back of the orbit, which has connections with both the external carotid and cerebral circulation. In addition, several arteries held to be present in primitive eutherians,

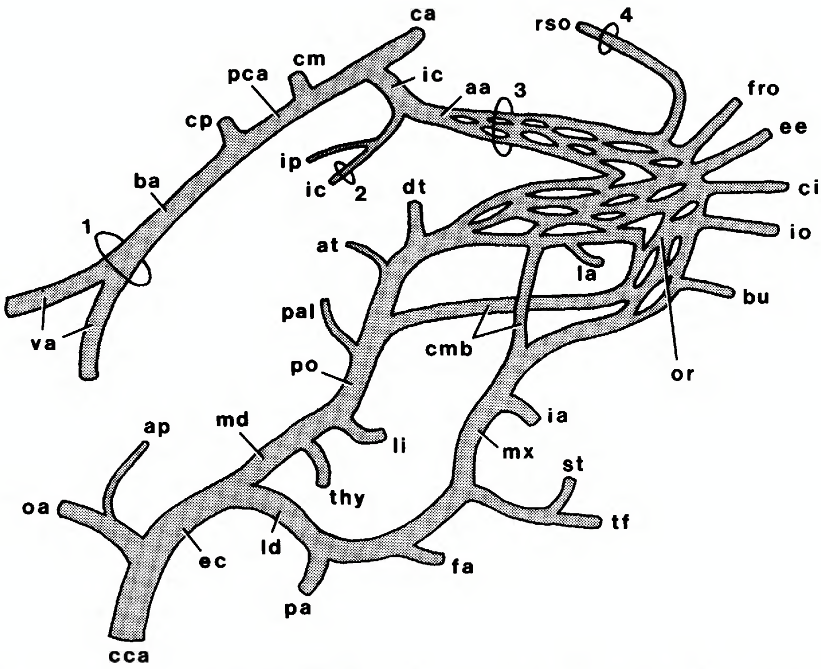

Fig. 2. Diagrammatic representation of the major cranial arteries in the fetal colugo *Cynocephalus* sp. (DUCEC 8310). Additional branches of the occipital artery are shown in figs. 3D and 4D. Vertebral arteries are shown as paired; all others are paired with the exception of the basilar. Numbers are for the following foramina: 1, foramen magnum; 2, carotid foramen; 3, confluent superior orbital fissure and foramen rotundum; 4, foramen between parietal and orbital-parietal commissure.

such as the internal carotid and stapedial (fig. 7A, C), are essentially absent. The areas usually supplied by these vessels are fed through the vertebral and external carotid arteries. Because an internal carotid does not arise from the common carotid, the origin of the occipital artery was chosen, for descriptive purposes, as the boundary between the common carotid and external carotid arteries.

The courses of the basicranial arteries in DUCEC 8310 are illustrated in ventral and lateral views in figures 3D and 4D, with the neighboring osseous and cartilaginous elements shown in figures 3A, B and 4A, B.

OCCIPITAL ARTERY

The well-developed occipital artery supplies a large distributional area including, in addition to the occiput, the pharynx, the meninges, and the side wall of the braincase. Originating where the common carotid passes medial to the hypoglossal nerve beneath the ear region, the occipital artery runs posteriorly, medial to the second arch (Reichert's) cartilage and associated styloid musculature (fig. 3D). Just beyond its origin, two branches arise from the occipital artery. The first is the medially directed ascending pharyngeal artery, which supplies a laryngeal branch before reaching to the posterodorsal surface of the pharynx. The second is a laterally directed muscular branch to the neighboring digastric and styloid musculature. The occipital artery then passes medial to the vagus nerve beneath the jugular foramen (lateral to the vagus in Specimens 1 and 4) and divides into medial and lateral branches, which rejoin further posteriorly to supply deep neck muscles. The larger lateral branch is treated as the main stem of the occipital artery, because it follows the course of the occipital artery of human anatomy passing immediately medial to the origin of the digastric muscle from the mastoid (Williams et al., 1989). Arising from the lateral branch (the occipital's main stem) are a second muscular branch to the digastric and styloid muscu-

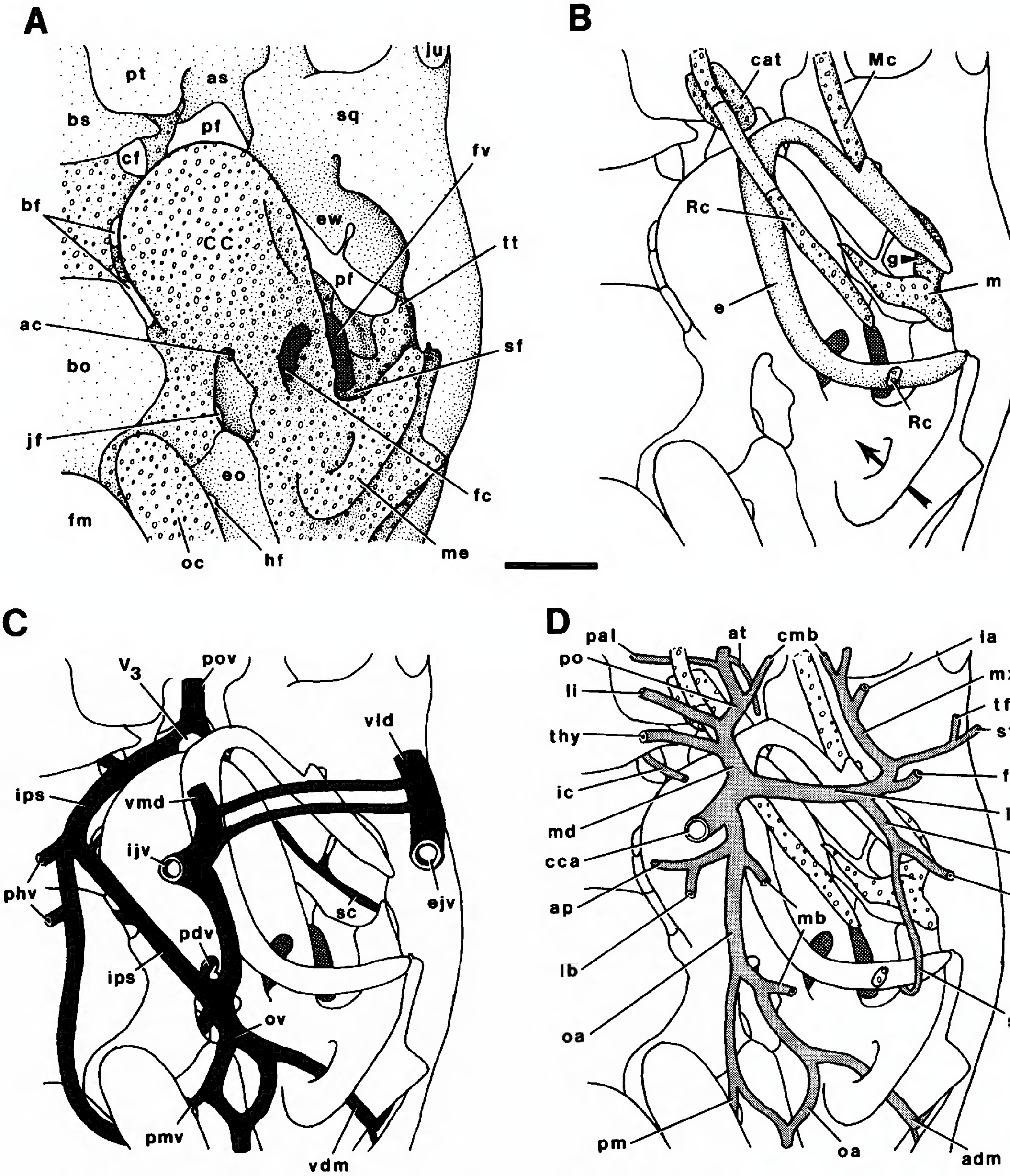

Fig. 3. Left basicranium of fetal *Cynocephalus* sp. (DUCEC 8310) in ventral view. **A**, Cartilages (open circles) and endochondral and intramembranous ossifications of the tympanic region with the auditory ossicles and tympanic floor elements removed. **B**, As above but with the floor elements and malleus in place. Arrow passes through vascular canal in mastoid eminence. **C**, Major veins in black. Veins accompanying the two divisions of the external carotid a. are cut for simplification. **D**, Major arteries in gray. Scale bar = 1.5 mm.

lature and an artery that runs on the side wall of the braincase, the arteria diploëtica magna (described below). The medial branch of the occipital supplies a posterior meningeal artery that enters the cranial cavity via the hypoglossal foramen.

Since its initial description in the echidna by Hyrtl (1853), the arteria diploëtica magna has been found to be a major vessel of the side wall of the braincase in many mammals, occupying a longitudinal channel, the posttemporal canal, between the auditory capsule and squamosal bone (Wible, 1987). In DUCEC 8310, the arteria diploëtica magna arises from the occipital artery and passes laterally through a canal in the pronounced mastoid eminence (fig. 3B, D). Beyond this canal, which opens on the lateral surface of the auditory capsule, the a. diploëtica magna runs dorsally posterior to the prominence of the lateral semicircular canal and then moves forward superior to that prominence, under cover of the squamosal bone (fig. 4D). At the point where the artery turns forward, a small branch is sent off posterodorsally deep to the squamosal. Near the rostral limit of the canalicular part of the auditory capsule, the a. diploëtica magna divides into a branch that runs forward into the meninges dorsolateral to the facial and trigeminal ganglia and a branch that moves dorsally and posteriorly between the lamina parietalis and parietal bone. The latter sends a tiny meningeal branch into the cranial cavity via one of the five openings between the lamina parietalis and auditory capsule (fig. 4B). This opening also transmits the capsuloparietal emissary vein of Gelderen (1924) (fig. 4C) and, therefore, is a capsuloparietal foramen (foramen jugulare spurium).

The course of the a. diploëtica magna on the side wall of the braincase differs somewhat in the other colugos. In Specimen 1, the artery runs within a deep groove on the mastoid eminence and not within a closed canal. It is unclear whether this represents individual variation or whether closure of the canal is a later ontogenetic event; the canal is closed in the juveniles, Specimens 3 and 4 (fig. 6), and in adult skulls. In Specimens 3 and 4, the entire a. diploëtica magna is covered laterally by the squamosal (fig. 6); in the fetal stages, the segment of the artery behind the prominence of the lateral semicircular canal is exposed laterally (fig. 4A, D). This lateral closure in the juveniles results from the expansion of the squamosal posteriorly and inferiorly toward the mastoid eminence. The lamina parietalis has also resorbed in the juveniles, so that the segment of the artery running dorsal to the auditory capsule courses through and supplies the meninges. Finally, in Specimen 4, a segment of the medial wall of the posttemporal canal, which is formed by the ossified auditory capsule (petrosal bone) in the juveniles, has resorbed. This results in a broad communication between the posttemporal canal and the subarculate fossa, the depression on the intracranial surface of the auditory capsule that accommodates the paraflocculus of the cerebellum (fig. 5A). Only a layer of connective tissue separates these two spaces. No arteries pierce this connective tissue, but a small vein drains from the subarcuate fossa into the companion veins of the a. diploëtica magna.

The number of openings between the lamina parietalis and auditory capsule varies among the fetal colugos studied here and those reported elsewhere. Whereas five openings occur in DUCEC 8310 (fig. 4B), only two are found, with the posterior one representing the capsuloparietal foramen, in Specimen 1 and in the 63-mm CRL *C. volans* modeled by Halbsguth (1973). The 28-mm CRL colugo described by Henckel (1929) has only a single large opening that nearly completely separates the lamina parietalis from the auditory capsule. As stated above, the lamina parietalis is lacking in the juveniles.

External Carotid Artery

Beyond the origin of the occipital artery, the external carotid divides into medial and lateral divisions, both of which terminate in the orbital rete (fig. 2). The medial division runs forward medial to the styloglossus and digastric muscles. The lateral division, on the other hand, moves laterally between these muscles and then forward on their lateral surfaces.

The first branch of the lateral division, the posterior auricular artery, arises lateral to the digastric, beneath the anterior crus of the ectotympanic (fig. 3D). It supplies the parotid gland, a cervical branch, and a small stylomastoid artery, which enters the tympanic cavity with the facial nerve to feed the stapedius muscle. The lateral division next gives off a facial artery and a common trunk for the transverse facial and superficial temporal arteries immediately behind the mandible. Moving forward between the mandible and the first arch (Meckel's) cartilage, the lateral division—now properly the maxillary ar-

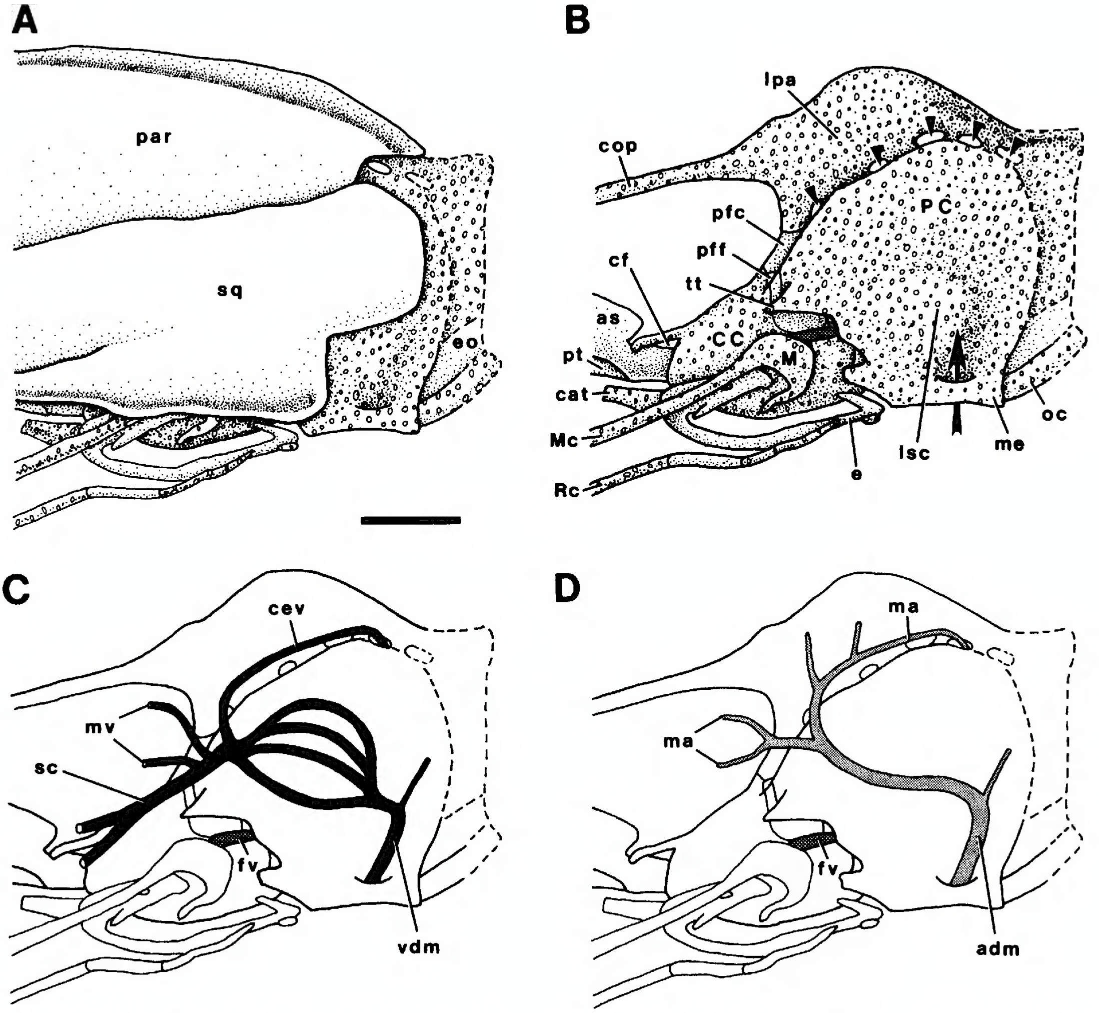

Fig. 4. Left basicranium of fetal *Cynocephalus* sp. (DUCEC 8310) in lateral view. **A**, Cartilages (open circles) and endochondral and intramembranous ossifications of the side wall of the braincase. Back of head was missing and the posterior chondrocranium is recreated here with dashed lines based on prenatal *C. volans* described by Halbsguth (1973). **B**, As above but with squamosal and parietal removed. Arrow passes through canal in mastoid eminence. Arrowheads point to openings between the auditory capsule and lamina parietalis. **C**, Major veins in black. **D**, Major arteries in gray. Scale bar = 1.0 mm.

tery—sends an inferior alveolar artery in the mandibular canal and divides into two terminal branches to the orbital rete. The larger branch reaches the back of the orbit passing ventrolateral to the lateral pterygoid muscle; the smaller is a communicating branch to the pterygoorbital artery (described below) that runs dorsal to the lateral pterygoid.

The medial division of the external carotid sends off superior thyroid and lingual arteries before ending as the pterygoorbital artery. Originally described in the rabbit by Fuchs (1905), the pterygoorbital artery parallels the course of the maxillary artery, but whereas the maxillary runs lateral to Meckel's cartilage, the pterygoorbital is medial (fig. 3D). From its origin, the pterygoorbital artery of the colugo runs anterodorsally between the ossified portion of Reichert's cartilage and the styloglossus muscle. After sending a small ascending palatine artery off medially to the soft palate, the pterygoorbital artery moves between the tensor veli palatini and medial pterygoid, supplying those muscles and a communicating branch to the maxillary artery that reaches the orbital rete by passing ventrolateral to the lateral pterygoid. The main stem of the pterygoorbital artery contacts the alisphenoid in front of the piriform fenestra and runs forward dorsal to the lateral pterygoid muscle into the orbital rete. Arising from the pterygoorbital artery beneath the alisphenoid are a deep temporal artery (fig. 2) and a small branch (**at** in fig. 3D) that moves posteriorly lateral to the mandibular division of the trigeminal nerve (discussed below).

The latter branch of the pterygoorbital artery in the juveniles supplies intracranial and tympanic branches (fig. 6A). The intracranial branch enters the cranial cavity via the anterior part of the foramen ovale and reaches forward into the orbital rete with the maxillary division of the trigeminal nerve. In an earlier report that included preliminary observations on the colugo (Wible, 1987), this vessel was identified as a ramus anastomoticus. However, it is now clear that this vessel lacks a meningeal branch and therefore is not a ramus anastomoticus. A similar, but more substantial vessel connects the maxillary artery to the orbit in mega- and microchiropterans (Wible, 1984, 1987). The tympanic branch of the pterygoorbital artery runs posteriorly into the tympanic cavity with the lesser petrosal nerve passing through a small gap between the ectotympanic and the epitympanic wing of the squamosal. In its course, the tympanic branch resembles the anterior tympanic artery of human anatomy, which is a branch of the maxillary artery (Williams et al., 1989). According to MacPhee and Cartmill (1986), the human anterior tympanic artery is the distal segment of the ramus inferior of the stapedial, but Diamond (1991) argued effectively, reiterating Tandler's (1902) position, that the ramus inferior is retained in humans as the stem of the middle meningeal artery. Until ontogenetic continuity with the ramus inferior is confirmed for the colugo by the study of earlier stages, I call this vessel an anterior tympanic artery.

CEREBRAL CIRCULATION

Reconstruction of the vertebral arteries in figure 2 is based on the juvenile colugos; these vessels are not known for the fetal specimens because the back of the cranial base is missing. The basilar artery, formed by the union of the vertebrals in the cranial cavity, supplies paired posterior cerebellar and posterior communicating arteries. Branches of the latter include anterior cerebellar, the posterior, middle, and anterior cerebrals, and a distal remnant of the internal carotid artery that enters the cavernous sinus in front of the hypophysis. Within the cavernous sinus the internal carotid remnant divides into anterior and posterior branches. The much larger anterior branch is equivalent to the arteria anastomotica described for the domestic cat by Davis and Story (1943), which connects the cerebral and orbital circulation via a course with the ophthalmic division of the trigeminal nerve. In the colugo, the arteria anastomotica breaks up into 4 or 5 smaller vessels that leave the cranial cavity via the confluent superior orbital fissure/foramen rotundum between the orbito- and alisphenoid and enter the orbital rete. The smaller posterior branch of the internal carotid remnant has two terminal twigs: a medial one that runs posteriorly within the cranial cavity dorsomedial to the inferior petrosal sinus and a lateral one that exits the cranial cavity with the internal carotid nerve via the carotid foramen (fig. 3D). The latter, the true continuation of the internal carotid artery, does not reach the surface of the cochlear housing. In the juvenile colugos, in which a complete auditory bulla is present, the distal internal carotid remnant becomes enclosed in a canal with the internal carotid nerve between the anterior pole of the promontorium and the bulla (fig. 6; Wible and Martin, 1993). The part of the bulla flooring this canal is formed by the fused tubal cartilage and entotympanic elements.

ORBITAL RETE

Three major arteries contribute to the formation of the orbital rete: the arteria anastomotica, the maxillary artery (with its communicating branch to the pterygoorbital), and the pterygoorbital artery (with its communicating branch to the maxillary) (fig. 2). As each of these approaches the back of the orbit, it breaks into 4 or 5 smaller vessels. These vessels, in turn, converge, intermingle, and freely anastomose with each other between the ophthalmic and maxillary nerves behind the eyeball. The bulk of the orbital rete is

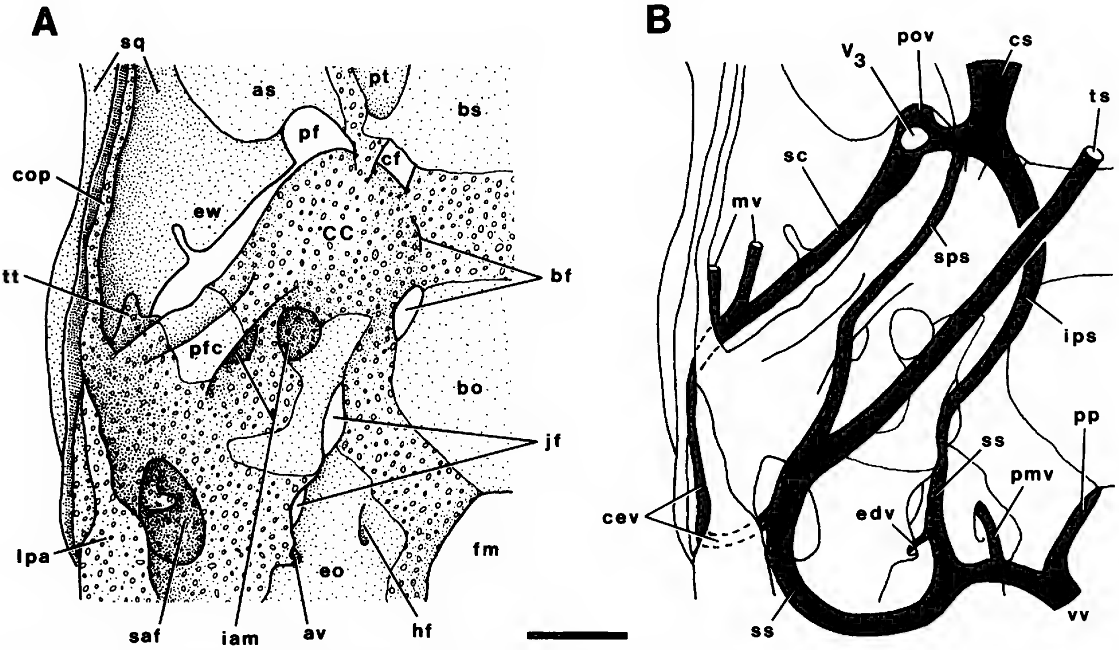

Fig. 5. Left basicranium of fetal *Cynocephalus* sp. (DUCEC 8310) in dorsal view with overlying parietal bone removed. **A**, Cartilages (open circles) and endochondral and intramembranous ossifications of the tympanic region. Though it appears bipartite, the jugular foramen is a single opening. **B**, Major veins in black. Transverse sinus does not contact the auditory capsule, but runs in the medial edge of the tentorium cerebelli. Course of sigmoid sinus and vertebral veins based on Specimens 3 and 4. Scale bar = 1.0 mm.

extracranial; only a small part extends intracranially into the cavernous sinus as the arteria anastomotica.

The orbital rete supplies the following terminal branches of the cranial arterial system: the lacrimal, external ethmoidal, frontal, ciliary, infraorbital, and buccal arteries (fig. 2). In addition, there is a small anterior meningeal branch of the orbital rete that enters the anterior cranial fossa between the orbitoparietal commissure and the parietal bone (between the orbitosphenoid and parietal in Specimen 4). This vessel probably represents the retained distal remnant of the ramus superior of the stapedial artery—the ramus supraorbitalis—and the opening by which it enters the cranial cavity is the cranio-orbital foramen (Wible, 1987).

VEINS

Diagrammatic representations of the major extra- and intracranial veins of the basicranium of *Cynocephalus* sp. (DUCEC 8310) are shown in figures 3C, 4C, and 5B with the associated bones and cartilages in figures 3A, B, 4A, B, and 5A. The most notable difference from the pattern held to be present in primitive eutherians (fig. 7B) is the absence of a postglenoid vein, which exits the skull via a postglenoid foramen and joins the external jugular vein. Most of the venous blood from the cranial cavity in the fetal colugo returns to the thorax in the internal jugular vein; vertebral veins, which are the most prominent channels in the juveniles, are not known for the prenatal stages as the back of the cranial base is missing. An external jugular vein is present, but it mainly drains superficial cranial structures. With few exceptions, the remaining major cranial veins in the fetal specimens are not single large channels, but are composed of several smaller vessels traveling together. This is altered in the juveniles, where most of the major veins are single channels.

SINUSES OF THE DURA MATER

Running posteriorly in the attached dorsal edge of the falx cerebri is the unpaired superior sagittal sinus. The paired transverse sinuses emerge from the superior sagittal sinus behind the cerebral hemispheres and move posteroventrally within the medial edges of the tentorium cerebelli. At the ventral margin of the tentorium, each transverse sinus connects with the superior petrosal sinus and bends posteriorly dorsal to the subarcuate fossa of the auditory capsule (fig. 5B). Here it divides into two unequal distributaries: the smaller capsuloparietal emissary vein (petrosquamous sinus) and the larger sigmoid sinus. The capsuloparietal emissary vein moves laterally exiting the cranial cavity via one of the five openings between the lamina parietalis and auditory capsule, the capsuloparietal foramen (fig. 4C). The vein runs forward in the space between the lamina parietalis and the overlying squamosal and leaves the skull via the vena diploëtica magna (see below). The sigmoid sinus turns inferiorly behind the subarcuate fossa and drains out the jugular foramen with the intracranial inferior petrosal sinus and out the foramen magnum into the vertebral vein (based on Specimens 3 and 4) (fig. 5B). Tributaries of the sigmoid sinus include the vein accompanying the endolymphatic duct in the vestibular aqueduct and the vein accompanying the posterior meningeal artery in the hypoglossal foramen.

The paired cavernous sinuses lie lateral to the hypophysis in the floor of the middle cranial fossa, extending from the orbital foramina to the front of the auditory capsules (fig. 5B). Each cavernous sinus communicates rostrally with an ophthalmic plexus of veins that is associated with the orbital rete via the confluent superior orbital fissure/foramen rotundum and caudally with, from medial to lateral, the inferior petrosal sinus, superior petrosal sinus, and sinus communicans (fig. 5B). Medially, the two cavernous sinuses are connected by anterior and posterior intercavernous sinuses positioned anterior and posterior to the hypophysis, respectively.

The inferior petrosal sinus consists of two parallel channels running posteriorly from the cavernous sinus, one within the cranial cavity (fig. 5B) and the other extracranial (fig. 3C), dorsal and ventral to the basioccipital-auditory capsule contact, respectively. These two channels communicate via the carotid foramen, the anterior and posterior openings of the basicapsular fissure, and the jugular foramen (fig. 3C). The extracranial channel joins the sinus communicans (described below) and the vein accompanying the pterygoorbital artery beneath the piriform fenestra and the pharyngeal plexus medially (fig. 3C). The intracranial channel joins the sigmoid sinus (based on the juveniles) (fig. 5B), and these, in turn, send a vein out the jugular foramen (fig. 3C). The vein that accompanies the perilymphatic duct in the cochlear aqueduct is a tributary of the extracranial inferior petrosal sinus (fig. 3C).

The superior petrosal sinus extends between the transverse and cavernous sinuses, passing dorsal to the prefacial commissure and trigeminal ganglion (fig. 5B). It does not reach the cavernous sinus in the juveniles.

The sinus communicans of Diamond (1988, 1992) was named for the dural sinus in haplorhine euprimates running anteromedially from the capsuloparietal emissary vein within a sulcus between the petrosal and squamosal bones and exiting the skull via either the piriform fenestra or foramen ovale. The sinus communicans of the fetal colugo follows essentially the same pathway (fig. 5B); it communicates with the capsuloparietal emissary vein posteriorly, runs along or near the gap between the squamosal and auditory capsule, and exits the skull at the piriform fenestra, joining the vein with the pterygoorbital artery and the extracranial channel of the inferior petrosal sinus (fig. 3C). The course of this sinus is marked in adult skulls (e.g., AMNH 241703) by a large sulcus along the petrosquamous and petrosphenoid suture. The colugo sinus communicans differs from that of adult haplorhines in that it also joins the cavernous sinus (fig. 5B). However, this connection is reported for prenatal stages in humans (Diamond, 1988).

Growth and resorption of various skeletal elements modify the courses of several sinuses in the juvenile specimens. (1) Capsuloparietal emissary vein—Most of the course of the capsuloparietal emissary vein is intramural in the fetal stages, between the lamina parietalis and squamosal (figs. 4C, 5B). With the loss of the lamina parietalis in the juveniles, the capsuloparietal emissary vein has a wholly intracranial course. (2) Inferior petrosal sinus—The cartilages connecting the cochlear capsule with the basal plate and ba-

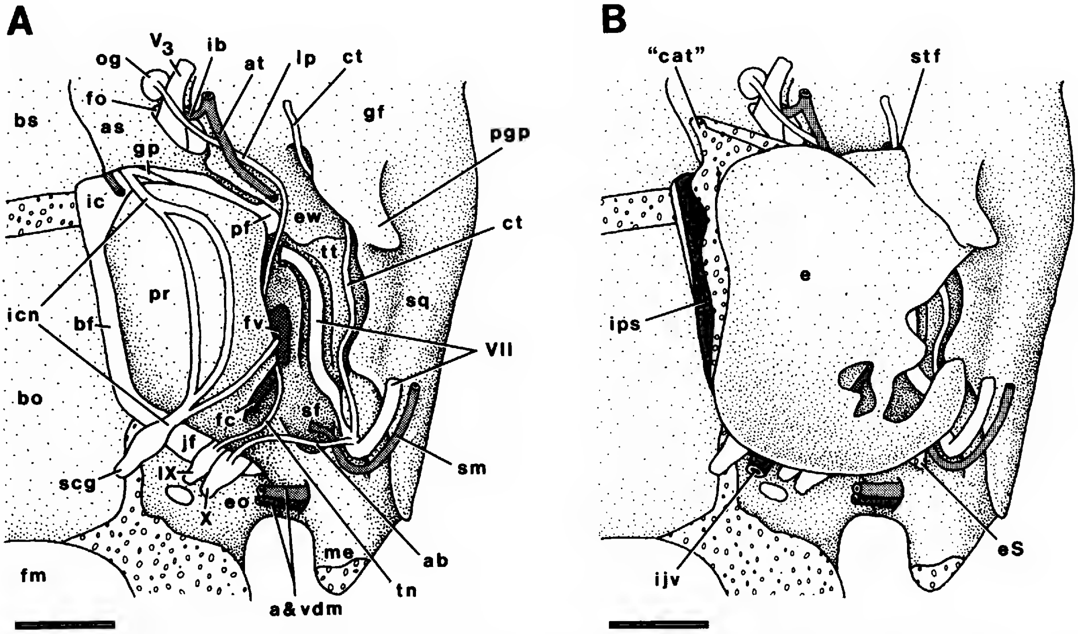

Fig. 6. Left basicranium of juvenile *Cynocephalus variegatus* (DUCEC 806a) in ventral view. **A**, Cartilages (open circles) and endochondral and intramembranous ossifications of the tympanic region: auditory ossicles and tympanic floor elements removed and selected nerves, arteries, and veins in place. The posterolateral branch of the internal carotid nerve joins the tympanic nerve lateral to the promontorium (not visible here) to form the lesser petrosal nerve. **B**, As above but with auditory bulla and extracranial channel of the inferior petrosal sinus in place. Fenestration in ectotympanic results from incomplete ossification and transmits no structures. The medial bullar wall forms a partial floor beneath the inferior petrosal sinus. Scale bar = 1.6 mm.

sioccipital in the fetuses (fig. 3A) are resorbed in the juveniles (fig. 6A). Remaining is a basicapsular fissure that is continuous anteriorly with the carotid foramen and posteriorly with the jugular foramen. The basicapsular fissure is not patent but is closed by connective tissue, which separates the persisting intra- and extracranial channels of the inferior petrosal sinus. With the formation of entotympanic elements in the medial bullar wall beneath the basicapsular fissure (Wible and Martin, 1993), a partial floor beneath the extracranial channel of the inferior petrosal sinus is created (fig. 6B). By the adult, the entotympanics have expanded medially, contacting the basioccipital and forming a complete osseous floor beneath the extracranial inferior petrosal sinus.

Other Head Veins

The internal jugular vein forms beneath the jugular foramen at the confluence of the extracranial inferior petrosal sinus, the occipital vein, and the vein draining the sigmoid sinus and intracranial inferior petrosal sinus (fig. 3C). The internal jugular moves forward medial to the vagus nerve, communicates with veins accompanying the medial and lateral divisions of the external carotid artery, and turns inferiorly into the neck with the common carotid artery (fig. 3C). The external jugular vein forms behind the mandible at the confluence of the veins accompanying the end branches of the lateral division of the external carotid artery (fig. 3C). It moves inferiorly into the neck behind the parotid gland, superficial to the sternomastoid muscle.

Veins accompany the arteria diploëtica magna in its course through the mastoid eminence and the side wall of the braincase (figs. 3C, 4C, 6). A single well-developed vein, the vena diploëtica magna, accompanies the proximal part of the artery, between its origin and where it disappears beneath the squamosal (fig. 3C). In the space between the au-

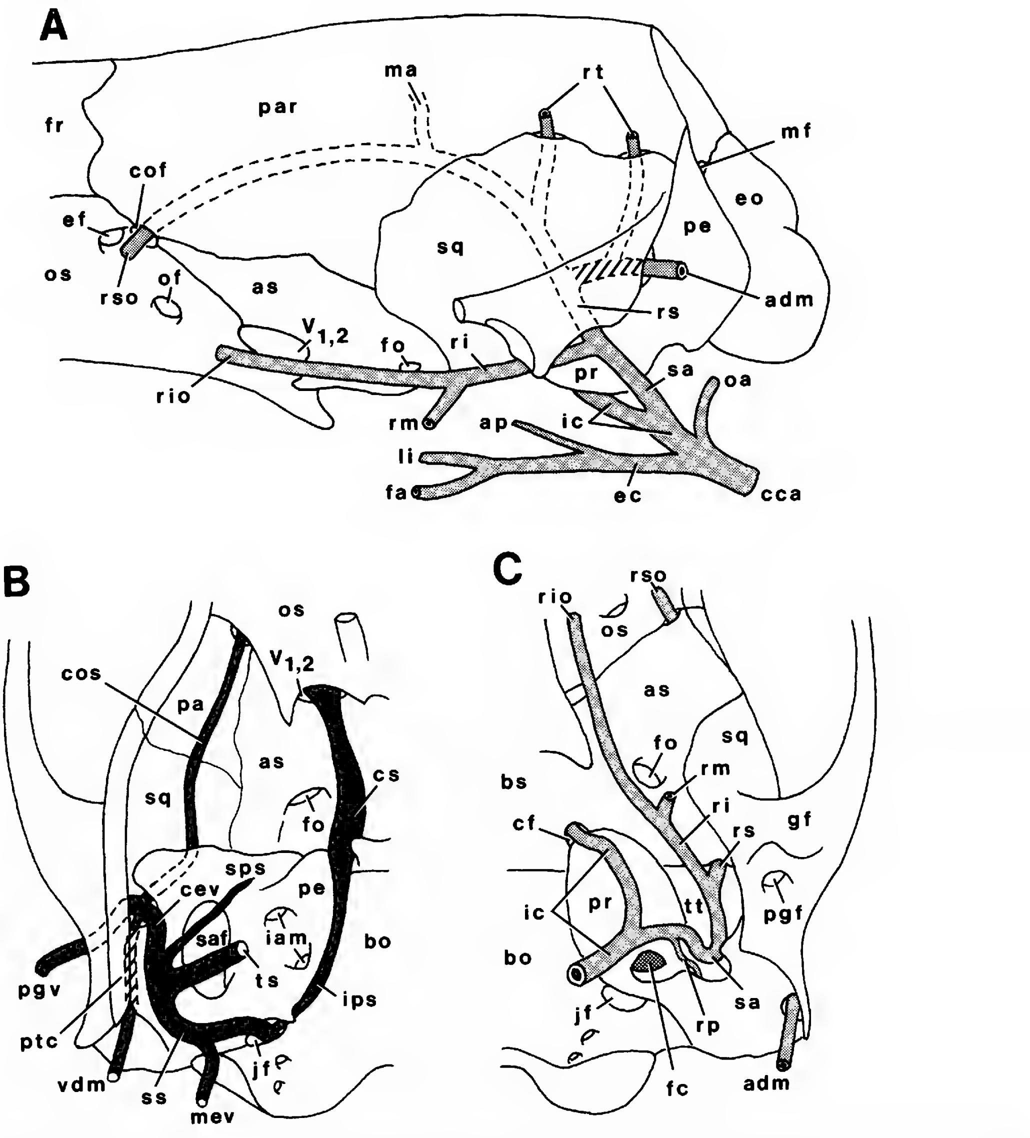

Fig. 7. Left braincase of a hypothetical primitive eutherian. A, Lateral view showing major cranial arteries, minus the cerebral circulation and vertebral arteries (after Wible, 1984, 1987). Gray = extracranial arteries; dashed lines = intracranial arteries; diagonal lines = segment of a. diploëtica magna in posttemporal canal. **B,** Dorsal view with skull roof removed showing major cranial veins (after Gelderen, 1924; Diamond, 1988, 1992). Diagonal lines = segment of v. diploëtica magna in posttemporal canal. C, Ventral view of tympanic floor and auditory ossicle removed showing major basicranial arteries in gray (after Wible, 1986, 1987). The internal carotid artery runs in a transpromontorial position beneath the promontorium.

ditory capsule and squamosal (the posttemporal canal), the vena diploëtica magna divides into 5–10 smaller veins, the majority of which run forward well dorsal to the arteria diploëtica magna (fig. 4C). These smaller veins reunite at the rostral end of the posttemporal canal to form one channel, which, in turn, divides into rostral and dorsal branches accompanying the end branches of the arteria diploëtica magna. The rostral branch is the sinus communicans; the dorsal branch is the capsuloparietal emissary vein. The vena diploëtica magna is a tributary of the occipital vein (fig. 3C).

COMPARISONS

The above descriptions are the first comprehensive account of the major cranial arteries and veins of the colugo. Several authors have remarked previously on particular aspects of the colugo cranial vasculature, with the most complete reports by Shindo (1915) and Gelderen (1924) on selected cranial veins in prenatal specimens. In the following, comparisons are made with these observations on colugos as well as with those on other mammals. For the purposes of comparison with other mammals, the observations made here are taken as representative of adult *C. variegatus* and *C. volans.* However, I remind the reader that the vascular pattern has only been studied in juveniles and the role of species-level variability was not investigated here.

To provide some background for the discussion, the principal components of the cranial arterial and venous patterns thought to be primitive for Eutheria are shown in figure 7. The arterial pattern is based on Wible (1984, 1986, 1987) and the venous pattern on Gelderen (1924) and Diamond (1988, 1992). Not all components of the cranial vasculature are compared below; discussion is limited largely to those vessels considered in previous phylogenetic analyses and whose incidence in extinct taxa can be reconstructed. Characters derived from the discussion are listed in table 1, and the distribution of these characters in archontans and other selected eutherians is shown in tables 1 and 2. For the sake of completeness, several characters unique to colugos among the taxa considered are included. In the following, the abbreviation CS refers to character and character state numbers in tables 1 and 2.

ARTERIES

INTERNAL CAROTID ARTERY

In dissections of ear regions of neonatal and adult *Cynocephalus volans,* Hunt and Korth (1980) found no evidence for any functional branch of the internal carotid artery. They did, however, find several nerves coursing on the ventral surface of the promontorium of the petrosal. The absence of the internal carotid artery from the colugo ear region is confirmed here (figs. 3D, 6A). Moreover, though not reported above, nerves run across the ventral surface of the cochlear housing in all specimens studied. Included are the internal carotid nerves (3–4 bundles), branches of the superior cervical ganglion (fig. 6A). The internal carotid nerves arise below the jugular foramen and enter the middle ear between the promontorium and auditory bulla at the level of the cochlear aqueduct, the opening for the perilymphatic duct (fig. 3A). They spread out on the promontorium, run forward, and reunite at the anterior pole, before exiting the middle ear via an opening between the promontorium and bulla.

In therian mammals, the internal carotid artery when present always accompanies the internal carotid nerves (Wible, 1984, 1986). Therefore, for therians in which the internal carotid artery is absent in the adult, the course of the internal carotid nerves indicates the artery's course before its developmental involution. From the location of the nerves, Wible (1986) characterized the colugo internal carotid artery as belonging to the transpromontorial type, the course considered to be primitive for Eutheria here (CS 1.0; fig. 7C).

Absence of the transpromontorial internal carotid artery along with its major intratympanic branch, the proximal stapedial, is unusual among eutherians, occurring in felid and hyaenid carnivorans in addition to colugos (Bugge, 1978), and in some artiodactyls (Wible, 1984), rodents (Bugge, 1974), and cheirogalied and lorisiform euprimates (MacPhee, 1981). Both the transpromontorial internal carotid and proximal stapedial are also thought to be lacking in some extinct taxa—some archaic primates (plesiadapids and paromomyids: MacPhee et al., 1983; MacPhee and Cartmill, 1986)—based on the absence of appropriate grooves, canals, and foramina. Kay et al. (1990) listed a partially involuted internal carotid system as a shared derived feature of dermopterans and some archaic primates (see also Kay et al., 1992). However, this characterization overlooks a significant difference. In colugos, the internal carotid nerves enter the middle ear posteromedially, at the level of the cochlear aqueduct, and run forward on the promontorium medial to the round window (fenestra coch-

TABLE 1

Vascular Characters and Character States of Some Eutherian Mammals[a]

1. Course of internal carotid artery and/or nerve
   1.0 transpromontorial (Wible, 1986) [*Cy*, Mi, Tu, Pt, St, Pa, Pl, Pg, some Ro, Ma, Ar, Li]
   1.1 in carotid canal formed by petrosal plate [Ha]
   1.2 in carotid canal formed by ectotympanic [Lp, some Ro]
   1.3 in carotid canal formed between entotympanic and petrosal [Me]
   1.4 extrabullar [Oc, some Ro]
2. Position of tympanic aperture of internal carotid artery and/or nerve
   2.0 posteromedial, by jugular foramen (Wible, 1986) [*Cy*, Mi, Tu, Pt, Lo, some An, Pg, some Ro, Ma, Ar, Li]
   2.1 posterolateral, by stylomastoid foramen [Le, Pa, Pl]
   2.2 anterior to fenestra cochleae [Me, *Ta*, some An, Lp, some Ro]
   2.3 aperture absent [Oc, some Ro]
3. Incidence of osseous carotid canal leading directly into carotid foramen
   3.0 absent (Wible, 1986) [La, some Ro, Ma, ?Ar, Li]
   3.1 present, in petrosal [St, Ha]
   3.2 present, between entotympanic and petrosal [*Cy*, Me, Mi, Tu, Pt]
   3.3 present, within ectotympanic [some Ro]
4. Incidence of proximal stapedial artery
   4.0 present (Wible, 1987) [some Me, Mi, Tu, Pt, some Lo, some Le, *Ta*, Pg, some Ro, Ma, some Ar, Li]
   4.1 absent [*Cy*, some Me, some Lo, some Le, An, Pa, Pl, La, some Ro, some Ar]
5. Course of ramus inferior of stapedial artery
   5.0 ventral to tegmen tympani (Wible, 1987) [Pt, some Ar, some Li]
   5.1 dorsal to tegmen tympani (Me, some Mi, Tu, Ha, La, some Ro, Ma, some Li]
   5.2 absent [*Cy*, some Mi, St, some Ro, some Ar, some Li]
6. Incidence of epitympanic crest on tegmen tympani
   6.0 absent (Wible, 1987) [*Cy*, Me, Mi, Ha, Pa, Pl, La, Ro, Ma, Ar, Li]
   6.1 present (Tu, Pt, St]
7. Incidence of arterial foramen in tegmen tympani
   7.0 absent (Wible, 1987) [*Cy*, Me, Mi, An, Pa, Pl, ?Ro, Ma, Ar, some Li]
   7.1 present, for proximal stapedial artery [Tu, St, *Ta*, La]
   7.2 present, for ramus superior of stapedial artery [Pt, some Li]
8. Incidence of foramina for ramus temporalis of stapedial artery
   8.0 present, in or near parietosquamosal contact (Wible, 1987) [Me, Mi, Tu, Pt, some Le, *Ta*, Pa, Pl, Pg, some Ro, Ma, Ar, Li]
   8.1 absent [*Cy*, Lo, some Le, An, La, some Ro]
9. Incidence of cranio-orbital foramen
   9.0 present, near the junction of the frontal, parietal, orbitosphenoid, and alisphenoid (Wible, 1987) [Me, Mi, Tu, Pt, some St, some An, some Ro, Ma, some Ar, Li]
   9.1 absent or very small [*Cy*, some St, *Ta*, some An, La, some Ro, some Ar]
10. Incidence of posterior opening into posttemporal canal
   10.0 present, between petrosal and squamosal (Wible, 1987) [La, some Li]
   10.1 present, within petrosal (mastoid eminence canal) [*Cy*]
   10.2 absent [Me, Mi, Tu, Pt, St, Ha, Ro, Ma, some Li]
11. Incidence of mastoid foramen
   11.0 present, on or near exoccipital-mastoid contact (Novacek, 1986) [?Me, ?Mi, Tu, St, Ha, Pa, Pl, Pg, La, some Ro, Ma, some Ar, ?Li]
   11.1 absent [*Cy*, Pt, some Ro, some Ar]
12. Incidence of maxillary artery
   12.0 absent (Wible, 1987) [La, some Ro, some Li]
   12.1 present, lateral to Meckel's cartilage and ventrolateral to lateral pterygoid muscle [*Cy*, St, Ha]
   12.2 present, lateral to Meckel's cartilage and medial to foramen ovale [Me, some Mi, Tu, Pt, some Ro, Ma, some Li]
   12.3 present, lateral to Meckel's cartilage and lateral to foramen ovale [some Mi, Ar]
13. Incidence of pterygoorbital artery
   13.0 absent (Wible, 1987) [Me, Mi, Tu, Pt, St, Ha, some Ro, Ma, Ar, Li]
   13.1 present [*Cy*, La, some Ro]
14. Course of ramus infraorbitalis
   14.0 ventral to alisphenoid (Wible, 1987) [*Cy*, some Mi, St, Ha, some Ro, Ar, Li]
   14.1 in alisphenoid canal [Tu, Pt, La, some Ro, Ma]
   14.2 intracranial [*Cy*, Me, some Mi, some Ro]
15. Incidence of arteria anastomotica
   15.0 absent (Wible, 1987) [Me, Mi, Tu, Pt, St, Ha, La, some Ro, Ma, Li]
   15.1 present [*Cy*, some Ro, Ar]
16. Incidence of orbital rete mirabile
   16.0 absent (McFarland et al., 1979) [Me, Mi, Tu, Pt, St, Ha, La, Ro, Ma, some Ar, Li]
   16.1 present [*Cy*, some Ar]
17. Exit of capsuloparietal emissary vein
   17.0 postglenoid foramen, within squamosal (Novacek, 1986) [Me, Mi, Tu, Pt, St, some An, Pa, Pl, Pg, Oc, some Ro, Ma, ?Ar, some Li]
   17.1 postglenoid foramen, between squamosal and petrosal [*Ta*, Lp, some Ro]
   17.2 absent [*Cy*, some An, some Ro, some Li]
18. Incidence of sinus communicans
   18.0 absent (Diamond, 1992) [some Mi, ?Tu, ?Pt, some St, some Ha, ?Ma, ?Ar, ?Li]
   18.1 present [*Cy*, ?Me, some Mi, some St, some Ha, ?La, ?Ro]
19. Contents of cranio-orbital sulcus
   19.0 ramus superior of stapedial artery with companion cranio-orbital sinus (Diamond, 1992)

TABLE 1—(*Continued*)

[Me, Mi, Tu, Pt, St, some Ha, some Ro, ?some Ar, Ma, Li]
19.1 cranio-orbital sinus [some Ha]
20.2 absent or vestigial [*Cy*, some St, some Ha, La, some Ro, some Ar]

[a] Sources for the primitive eutherian state (0) follow the state's description. Taxa abbreviations: An, Anthropoidea; Ar, Artiodactyla; *Cy*, *Cynocephalus*; Ha, Haplorhini; La, Lagomorpha; Le, Lemuriformes; Li, Lipotyphla; Lo, Lorisiformes; Lp, Leporidae; Ma, Macroscelidea; Me, Megachiroptera; Mi, Microchiroptera; Oc, Ochotonidae; Pa, Paromomyidae; Pg, Plagiomenidae; Pl, Plesiadapidae; Pt, Ptilocercinae; Ro, Rodentia; St, Strepsirhini; *Ta*, *Tarsius*; Tu, Tupaiinae. ? denotes taxon for which character distribution is not well known.

leae) (fig. 6A); this is the position of the tympanic aperture thought to be primitive for Eutheria (CS 2.0; fig. 7C). In contrast, in plesiadapids and paromomyids, the opening that is interpreted for the entrance of the internal carotid nerves is situated posterolaterally (CS 2.1), near the stylomastoid foramen, and the nerves run forward along or perhaps within a bridge of bone that connects the bullar wall to the back of the promontorium before reaching their transpromontorial position (MacPhee et al., 1983; MacPhee and Cartmill, 1986; Szalay et al., 1987; Kay et al., 1992). The latter is a rare course among eutherians, occurring elsewhere only in lemuriform euprimates (MacPhee, 1981, 1987). I contend that the position of the involuted internal carotid artery, as indicated by the nerve, is a character of more signifcance than the simple fact of involution, which has already been shown to vary, for example, within species of lemuriform euprimates (cf. Tandler, 1899; Conroy and Wible, 1978).

The distal remnant of the internal carotid artery is enclosed in a canal between the promontorium and the entotympanic component of the auditory bulla in the juvenile colugos studied here (fig. 6). As noted by Wible and Martin (1993), a similar osseous canal floored by the entotympanic transmits the internal carotid artery and nerve from the middle ear to the carotid foramen in scandentians, megachiropterans, and microchiropterans (CS 3.2). A course whereby the internal carotid artery and nerve do not pass

TABLE 2
Taxon-Character List[a]

Taxa	Characters 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Cynocephalus	0	0	2	1	2	0	0	1	1	1	1	1	1	0 & 2	1	1	2	1	2
Megachiroptera	3	2	2	0*	1	0	0	0	0	2	0	2	0	2	0	0	0	1	0
Microchiroptera	0	0	2	0	1*	0	0	0	0	2	0	2, 3	0	2*	0	0	0	0, 1	0
Tupaiinae	0	0	2	0	1	1	1	0	0	2	0	2	0	1	0	0	0	0	0
Ptilocercinae	0	0	2	0	0	1	2	0	0	2	1	2	0	1	0	0	0	0	0
Strepsirhini	0	0, 1	1	0*	2	1	1	0*	0*	2	0	1	0	0	0	0	0	0*	0
Haplorhini	1	0, 2	1	0*	1	0	0, 1	0*	0*	2	0	1	0	0	0	0	0*	1*	0*
Paromomyidae	0	1	?	1	?	0	0	0	?	?	0	?	?	?	?	?	0	?	?
Plesiadapidae	0	1	?	1	?	0	0	0	?	?	0	?	?	?	?	?	0	?	?
Plagiomenidae	0	0	?	0	?	?	?	0	?	?	0	?	?	?	?	?	0	?	?
Lagomorpha	2, 4	2, 3	0	1	1	0	1	1	1	0	0	0	1	1	0	0	0, 1	1	2
Rodentia	0*	0*	0*	0*	1*	0	0	0*	0*	2	0*	0*	0*	0*	0*	0	0–2	1	0*
Macroscelidea	0	0	0	0	1	0	0	0	0	2	0	2	0	1	0	0	0	0	0
Artiodactyla	0	0	0	0*	0*	0	0	0	0*	?	1*	3	0	0	1	0*	0	0	0*
Lipotyphla	0	0	0	0	0*	0	0*	0	0	0*	0	0*	0	0	0	0	0*	0	0

[a] Characters, character states, and distributions are described in table 1. Multistate taxa were handled in one of two ways. When a parsimonious inference was possible, it is denoted by an asterisk (*). When a parsimonious inference was not possible, all states are listed. ? denotes unknown condition.

through an osseous canal to reach the carotid foramen is thought to be primitive (CS 3.0).

STAPEDIAL ARTERY

The stapedial artery was responsible for supplying most of the tissues of the head outside the face, tongue, and pharynx in primitive eutherians (fig. 7A). This pattern is modified considerably in the colugo with the loss of the proximal part of the stapedial artery (CS 4.1) and the annexation of the terminal branches of the stapedial to the external carotid and cerebral circulation (fig. 2, 3D). Primitively, the stapedial artery has several large branches passing through the middle ear (fig. 7C). The only artery entering the middle ear in the colugo is the small stylomastoid artery, which annexes the area supplied by the ramus posterior of the stapedial (fig. 6A). Features of the intratympanic part of the stapedial system that vary among other archontans are the course of the ramus inferior with regard to the tympanic roof (CS 5.0,1), an epitympanic crest of the tegmen tympani housing the stapedial artery (CS 6.1), and an arterial foramen in the tegmen tympani (CS 7.1,2).

Two terminal branches of the stapedial system of primitive eutherians that are either insignificant or absent in colugos are the ramus temporalis and ramus supraorbitalis. Arising from the ramus superior or arteria diploëtica magna within the cranial cavity, the ramus temporalis (with accompanying veins) passes through opening(s) in the vicinity of the squamosal-parietal junction to supply the temporalis muscle (CS 8.0; fig. 7A). Such openings are absent in the sectioned colugos and in adult skulls surveyed (CS 8.1), and the temporalis muscle is supplied exclusively through branches of the external carotid. Absence of foramina for the ramus temporalis is rare at the ordinal level within Recent Eutheria, occurring in Hyracoidea (Wible, 1987) and Lagomorpha (unpubl. obs.) in addition to Dermoptera. However, these foramina have been lost independently numerous times within various orders (e.g., foramina are widely distributed among noncatarrhine euprimates but are seldom present in catarrhines; Diamond, 1991).

The eutherian ramus supraorbitalis, the rostral continuation of the ramus superior, enters the orbit (with accompanying veins) via a carnio-orbital foramen near the junction of the frontal, parietal, orbitosphenoid, and alisphenoid (CS 9.0; fig. 7A). In the sectioned colugos, a diminutive ramus supraorbitalis branches from the orbital rete and enters the cranial cavity via a small cranio-orbital foramen (CS 9.1; fig. 2). However, in a survey of 30 adult skulls in the AMNH, a cranio-orbital foramen occurred in only 15, including examples of *C. volans* and *C. variegatus*. The location and incidence of the cranio-orbital foramen has been found to be highly variable in some other Recent taxa (e.g., strepsirhine euprimates, Cartmill, 1978), but total absence of this opening is rare at the ordinal level, occurring in only Pholidota, Carnivora, Lagomorpha, and Hyracoidea (Wible, 1987).

ARTERIA DIPLOËTICA MAGNA

An arteria diploëtica magna (with accompanying veins) running in the space between the auditory capsule and squamosal (the posttemporal canal) is widely distributed among Recent mammals and is considered to be primitive for Mammalia and Eutheria (Wible, 1987; Rougier et al., 1992; fig. 7A). Therefore, the occurrence of this vessel in the colugo is not unique. However, what is unique to the colugo among mammals is the course of the artery through a canal in the mastoid eminence (CS 10.1; figs. 3D, 4D, 6A). In other mammals, the artery runs medial to and then behind the mastoid eminence en route to the posttemporal canal, which generally opens on the occiput between the squamosal and petrosal (CS 10.0; fig. 7A). Some armadillos have a canal in the mastoid through which the a. diploëtica magna passes en route to the posttemporal canal (Tandler, 1899), but this is not equivalent to the colugo canal. The armadillo canal is not performed in cartilage (see Reinbach, 1952a, 1952b), presumably forming via appositional bone growth from the petrosal, and it lies posterior to the origin of the digastric muscle (unpubl. obs.). The colugo canal is preformed in cartilage and lies anterior to the digastric origin.

Hunt and Korth (1980) in their dissection of a neonatal *Cynocephalus volans* found no artery passing through the canal in the mastoid eminence identified here for the arteria diploëtica magna. They reported (p. 178) that "the position of the foramen on the exoccipital-mastoid suture and its connection to the posterior lacerate foramen (jugular foramen) suggest that it is a venous foramen, perhaps analogous to the mastoid venous foramen found in a more dorsal position on the exoccipital-mastoid suture in many mammals." (Whereas the external orifice of the foramen in question is on the exoccipital-mastoid suture in the adult colugo, there is an internal orifice that is wholly within the mastoid portion of the petrosal, as in the juveniles.) Cartmill and MacPhee (1980) independently arrived at a similar conclusion, suggesting that the canal in the colugo mastoid eminence is homologous with the mastoid foramina in other eutherians.

Mastoid foramina on the occiput are widely distributed among eutherians, usually between the exoccipital and mastoid, near the squamosal and/or parietal contact (CS 11.0; fig. 7A; Novacek, 1986). In the few instances where the occupant of the mastoid foramen is known, it is an occipital or mastoid emissary vein (e.g., *Canis,* Evans and Christensen, 1979; *Homo,* Williams et al., 1989). This emissary vein, which arises from the sigmoid sinus within the cranial cavity (fig. 7B), is not equivalent to the vena diploëtica magna of the colugo, which arises from the confluence of the capsuloparietal emissary vein and sinus communicans within the posttemporal canal and accompanies the arteria diploëtica magna (fig. 4C, D). Consequently, the mastoid foramen on the occiput of other eutherians is not equivalent to the mastoid eminence canal of the colugo. A mastoid emissary vein and mastoid foramen are wholly lacking in the colugo (CS 11.1). Mastoid foramina also are lacking in hyracoids, proboscideans, cetaceans, sirenians, and some artiodactyls (Novacek, 1986), rodents (Wahlert, 1985), and ptilocercines (Kay et al., 1992). Though mastoid foramina are found in living neoselenodonts, their absence is thought to be primitive for Artiodactyla (Coombs and Coombs, 1982).

The absence of the arteria diploëtica magna in the neonatal *C. volans* dissected by Hunt and Korth (1980) is surprising, given that the artery is well developed in the juveniles studied here, one of which (Specimen 3) may be *C. volans.* Perhaps this represents an extreme case of individual variation. Only additional study can address this observation.

MAXILLARY ARTERY

The distributional area of the external carotid artery was limited chiefly to the face, tongue, and pharynx in primitive eutherians (fig. 7A). In contrast, the external carotid serves a much larger area in most Recent eutherians. This transformation, which has occurred independently numerous times, is accomplished in most cases by the formation of an anastomosis between the external carotid and the ramus inferior of the stapedial near the foramen ovale (Wible, 1987). Five different types of such anastomoses, all of which are generally called maxillary arteries, are known to occur among Recent mammals (Wible, 1987). Colugos are unusual in that they have two types of anastomoses. The first, called the maxillary artery above, runs forward lateral to Meckel's cartilage and ventrolateral to the lateral pterygoid muscle (CS 12.2; fig. 3D); such an anastomosis is known to occur elsewhere only in the xenarthran *Tamandua,* euprimates, and marsupials (Wible, 1987). The second, the pterygoorbital artery above, also found in lagomorphs and some rodents (Wible, 1987), moves forward medial to Meckel's cartilage and the mandibular nerve (CS 13.1; fig. 3D).

RAMUS INFRAORBITALIS

The ramus infraorbitalis connects the ramus inferior of the stapedial or "maxillary" artery with the back of the orbit. In Recent eutherians, this vessel either lies on the ventral surface of the skull base, is enclosed in a canal in the alisphenoid, or runs dorsal to the skull base (Wible, 1987). Following Novacek (1986) and Wible (1987), it is accepted here that an alisphenoid canal was lacking and that the ramus infraorbitalis developed ventral to the ala temporalis (the chondrocranial precursor of the alisphenoid) in primitive eutherians (CS 14.0; fig. 7A, C). The juvenile colugos studied here are unusual in that there are connecting channels running both below and above the skull base; the former, the major pathway, includes the rostral continuations of the maxillary and pterygoorbital arteries and the latter is a branch of the diminutive anterior tympanic artery (fig. 6A). A dorsal pathway (CS 14.2) that passes through the foramen ovale (or a separate opening anterior to it) is reported elsewhere only in a mega- and microchiropterans (Wible, 1987). A dorsal pathway also occurs in dipodoid rodents, but the ramus infraorbitalis does not have a foramen of entrance into the cranial cavity as it is merely the rostral continuation of the intracranial ramus inferior (Wible, 1897).

Kay et al. (1992) distinguished two sorts of canals in the alisphenoid that transmit the ramus infraorbitalis or "maxillary" artery: in some forms, the canal is on the lateral side of the braincase and lateral pterygoid plate and in others, it is an opening in the lateral pterygoid plate. The existence of these two sort of canals is not disputed here, but I am unaware of any case in which the latter canal transmits the "maxillary" artery. Kay et al. (1992) cited *Tarsius, Tupaia,* and *Ptilocercus* as examples. According to Hill (1953), however, the "maxillary" artery in tarsiers runs wholly lateral to the lateral pterygoid plate. Moreover, the scandentian alisphenoid canal, which does transmit the "maxillary" artery (Cartmill and MacPhee, 1980; Zeller, 1986), is not truly an opening in the lateral pterygoid plate. It is more accurately described as between the lateral pterygoid plate and skull base, though the position of the canal's apertures is somewhat variable. Many scandentians (e.g., *Tupaia palawanensis,* FMNH 63004; *Urogale everetti,* FMNH 57308) have both an alisphenoid canal for the "maxillary" artery and an opening wholly within the lateral pterygoid plate, presumably for branches of the mandibular nerve, as in some rodents (Wahlert, 1985). Different sorts of alisphenoid canals for the "maxillary" artery may be distinguishable among eutherians based on their pattern of ontogenetic formation, e.g., within the chondrocranium versus between chondrocranial and dermal elements (Wible, 1987). Yet, because comparative knowledge of this region's ontogeny is limited, the term alisphenoid canal is used here for any bony passageway transmitting the "maxillary" artery from the infratemporal fossa to the orbit (CS 14.2).

ARTERIA ANASTOMOTICA

In addition to the colugo, an arteria anastomotica (CS 15.1) joining the intracranial part of the internal carotid to the orbit occurs in cetaceans, artiodactyls, and some xenarthrans, pholidotans, carnivorans, and rodents (Wible, 1984, 1987). Associated with the arteria anastomotica in cetaceans, artiodactyls, and some carnivorans is an intracranial rete mirabile, as described here for the colugo.

ORBITAL RETE

The orbital rete of the colugo (CS 16.1) resembles that described for the domestic cat (Davis and Story, 1943; Daniel et al., 1953). Both are largely extracranial, associated with the ophthalmic and maxillary nerves at the back of the orbit; both are fed by a maxillary artery and arteria anastomotica; and both are bathed in a venous lake, connected with the cavernous sinus and pterygoid plexus. The colugo orbital rete is not nearly as extensive in size and complexity as that of the cat and it is supplied by two "maxillary" arteries. Orbital retia with both intra- and extracranial components also occur in cetaceans (McFarland et al., 1979) and some artiodactyls (Daniel et al., 1953; Wible, 1984).

VEINS

Comparative information on the veins of the head among Recent mammals is, in general, more limited than is that on the cranial arteries, because the venous system has not been as intensively or widely investigated. Therefore, the following comparisons are more restricted in scope and more tentative in nature.

CAPSULOPARIETAL EMISSARY VEIN

The major outlet for the sinuses of the dura mater in most eutherians is the capsuloparietal emissary vein (petrosquamous sinus) (fig. 7B; Gelderen, 1924; Wible, 1990). This vein generally leaves the skull as the postglenoid vein via an opening within the squamosal (or between the squamosal and petrosal) behind the glenoid fossa, the postglenoid foramen (fig. 7C), and drains into the external jugular vein (CS 17.0,1).

The sectioned colugos studied here have a capsuloparietal emissary vein, but its major outlets are the sinus communicans and vena diploëtica magna (fig. 4C). No venous drainage was found passing through a postglenoid foramen in these specimens (CS 17.2) or in the prenatal *C. volans* described by Shindo (1915) and Gelderen (1924). Several authors, however, have reported that a postglenoid foramen is present in adult colugos. Cartmill and MacPhee (1980: 127) stated that the postglenoid foramen is "tiny or absent," and according to Novacek (1986: 86), it is "concealed ventrally by trabeculated flattened auditory bulla." A full evaluation of these statements is not possible, because neither Cartmill and MacPhee nor Novacek illustrated the opening in question. Yet, it is possible that the opening to which these authors refer is the squamotympanic fissure, the only opening behind the glenoid fossa in the adult colugo skulls studied in the AMNH. The squamotympanic fissure, which gives passage to the chorda tympani nerve in the juveniles (fig. 6B), lies posteromedial to the glenoid fossa, as would a postglenoid foramen, and is of variable size in adult skulls. The opening that Russell (1964: fig. 20A) labeled as a postglenoid foramen for the colugo is the squamotympanic fissure of this report.

The postglenoid foramen has been reported to be absent in various extant and extinct eutherians (see Cope, 1880; Novacek, 1986). However, I caution that absence of a discrete postglenoid foramen within the squamosal does not necessarily require absence of a postglenoid vein, because, for example, in the rat this vessel leaves the skull via a gap between the squamosal and petrosal (Greene, 1935). Therefore, dissections must be completed to ascertain the incidence of a postglenoid vein in those taxa which lack a postglenoid foramen in the squamosal but have a large gap between the squamosal and petrosal, such as in soricids (McDowell, 1958). Of the few eutherians for which the venous system has been studied, a postglenoid vein (and foramen) is absent in the cat *Felis* (Dennstedt, 1904), the sloth *Bradypus,* and hyrax *Hyrax* (Gelderen, 1924), the aardvark *Orycteropus* (Thewissen, 1985), and most humans (Diamond, 1992). This spotty distribution argues for multiple losses of this vessel.

SINUS COMMUNICANS

In addition to the colugo, a sinus communicans (CS 18.1) has been reported to date only in haplorhine euprimates and several rodents (i.e., *Mesocricetus, Sciurus,* and *Rattus*) (Diamond, 1992). It is also present in late-fetal and juvenile specimens of the rabbit *Oryctolagus* and late-fetal specimens of the megachiropteran *Pteropus* and *Rousettus* and the microchiropteran *Myotis* (unpubl. obs.); I tentatively score the sinus communicans as present for these groups. The incidence of the sinus communicans in adult bats has not been confirmed, and Diamond (1992) did not report it for adult *Carollia.* The sinus communicans of the colugo differs from that of the above forms in that it is not accompanied by an intracranial ramus inferior of the stapedial artery; this also occurs frequently in *Tarsius* and occasionally in some platyrrhines (Diamond, 1992). Among extinct forms, a large sulcus along the petrosquamous and petrosphenoid sutures, like that containing the sinus communicans in the colugo, is found in the lemuriform euprimate *Paleopropithecus* (Diamond, 1992).

Neither Shindo (1915) nor Gelderen (1924) described a sinus communicans in the prenatal colugos they investigated. However, these reports only concern selected cranial veins and do not treat the entire system.

CRANIO-ORBITAL SINUS

Many extant eutherians have a groove on the intracranial surface of the side wall of the braincase extending posteriorly from the cranio-orbital foramen. The major occupant of this groove, the cranio-orbital sulcus or sinus canal, in most forms is the ramus superior of the stapedial artery (CS 19.0), which is accompanied by small veins, a cranio-orbital sinus (fig. 7A, B; Kielan-Jaworowska et al., 1986; Diamond, 1992). In some euprimates, however, the cranio-orbital sinus is either the sole or the major occupant of this sulcus (CS 19.1; Diamond, 1992). Only the posteriormost part of the cranio-orbital sinus is present in the colugos studied here, represented by the dorsal meningeal branch of the sinus communicans (fig. 4C). Yet, a complete cranio-orbital sinus is apparently present in some adults, given that a diminutive cranio-orbital sulcus (CS 19.2) extends between the groove for the sinus communicans and cranio-orbital foramen in some skulls (e.g., AMNH 241703).

VENA DIPLOËTICA MAGNA

In macerated adult colugo skulls, Cartmill and MacPhee (1980) noted that the canal between the squamosal and petrosal identified here as the posttemporal canal communicates with the subarcuate fossa, the depression on the intracranial surface of the petrosal which accommodates the paraflocculus of the cerebellum. They speculated that this represents a major route for venous drainage. In Specimen 4 of this report, the part of the petrosal bone separating the subarcuate fossa and posttemporal canal has resorbed, but connective tissue separates the two spaces and only a small vein drains through it into the vena diploëtica magna.

As Kielan-Jaworowska et al. (1986) observed, fenestration of the subarcuate fossa is rare among modern mammals. They found it, including transmitted veins, in embryos of some microchiropterans and elephant shrews. Cartmill et al. (1981) found a patent canal leading from the depths of the subarcuate fossa to the sigmoid sinus in some anthropoid euprimates (i.e., nonateline ceboids), which included a dried vessel in one *Saguinus* skull. The distribution of fenestration of the subarculate fossa has not been studied here and is not included in tables 1 and 2.

INFERIOR PETROSAL SINUS

In modern eutherians, the inferior petrosal sinus exits the skull via either the carotid foramen, basicapsular fissure, or jugular foramen resulting in courses that are largely extracranial or intracranial (Wible, 1983). Which of these patterns is primitive for Eutheria is uncertain, because the course of this sinus has not been widely investigated. The inferior petrosal sinus of the colugo is remarkable in that it has extra- and intracranial channels separated by connective tissue, with the extracranial one floored by the entotympanic, basioccipital, and petrosal. Presence of two channels is not unique to the colugo. *Canis,* for example, has extra- and intracranial veins running medial to the ear region (Evans and Christensen, 1979; Wible, 1983), and the extracranial one passes through a canal between the entotympanic, basioccipital, and petrosal (though this canal also gives passage to the internal carotid artery). Because the course of the inferior petrosal sinus has not been studied for most taxa in table 2, it is not included.

According to Kay et al. (1992), contact between the entotympanic and basioccipital is unique to colugos and the paromomyid *Ignacius.* It is not known whether this shared morphology also includes the formation of the floor beneath the inferior petrosal sinus by the entotympanic-basioccipital contact in *Ignacius,* as occurs in colugos. Wible and Martin (1993) already have remarked that contact between the entotympanic and basioccipital is not unique to colugos and *Ignacius,* but also occurs in tupaiines, palaeanodonts, some xenarthrans and carnivorans, and perhaps in plagiomenids.

CONCLUSIONS

In most features of the cranial circulation, colugos are highly derived compared to the pattern reconstructed for primitive eutherians (table 2). Moreover, colugos exhibit several autapomorphies among mammals, including a canal in the mastoid eminence for the arteria and vena diploëtica magna and cooccurrence of a maxillary artery running ventrolateral to the lateral pterygoid muscle and a pterygoorbital artery. With such a highly derived cranial vascular pattern, colugos, not surprisingly, share derived features with a variety of other eutherians, including extinct taxa that have been included within Dermoptera and Recent orders that are relevant to the superordinal hypotheses shown in figure 1. Rather than generate new phylogenetic hypotheses from the very limited data set presented here, I have chosen to evaluate the evidence for colugo affinities from the cranial vasculature with regard to hypotheses published previously.

PLAGIOMENIDAE AND ARCHAIC PRIMATES

In their review of the craniodental evidence for plagiomenid relationships, MacPhee et al. (1989) found no features of the cranial vasculature allying plagiomenids with colugos or distinguishing plagiomenids from primitive eutherians. My descriptions of the colugo vascular pattern have not altered MacPhee et al.'s conclusions, but from the amount of missing data scored for plagiomenids in table 2, I reiterate that we know few details of their cranial vasculature.

In support of a clade composed of colugos, paromomyids, and plesiadapids, Kay et al. (1992) offered four features, including two from the cranial circulation—absence of a transpromontorial internal carotid artery, absence of a stapedial artery, ossified external auditory meatus, and entotympanic contacting basioccipital. As argued here, the position of the internal carotid artery before involution is a more significant character than involution itself. The colugo internal carotid artery is in the transpromontorial course thought to be primitive for Eutheria (CS 1.0, 2.0), whereas that in paromomyids and plesiadapids has shifted its position posterolaterally from the promontorium, exhibiting a pathway found elsewhere only in some strepsirhine euprimates (CS 2.1). Given this positional difference, I do not find absence of a transpromontorial internal carotid artery a convincing character allying colugos with archaic primates. The other three features offered by Kay et al. (1992) are by no means unique to colugos and archaic primates.

SUPERORDINAL RELATIONSHIPS

Regarding the archontan hypothesis in figure 1A, no derived features of the cranial vasculature distinguish all archontans from other eutherians. The feature closest to an archontan synapomorphy is the presence of an osseous carotid canal beneath the carotid foramen, but the canal is formed by the petrosal in euprimates (CS 3.1) and lies between the entotympanic and petrosal in the remaining extant archontan taxa (CS 3.2). The sister-group relationship between colugos and bats predicted by Novacek and Wyss (1986) based largely on postcranial similarities is supported by a course for the ramus infraorbitalis through the foramen ovale (or an opening anterior to it) and dorsal to the alisphenoid (CS 14.2). This arterial pathway was proposed previously as a chiropteran synapomorphy (Wible and Novacek, 1988), but its discovery in the colugo adds further support to a colugo + bat clade. A sinus communicans (CS 18.1) is also shared by the colugo and some bats (along with rodents, lagomorphs, and haplorhine euprimates) and may represent a synapomorphy of a colugo + bat clade. However, the distribution of this vessel among the taxa considered here is poorly known.

Regarding the diphyletic chiropteran hypothesis in figure 1B, no derived features of the cranial circulation are shared by colugos, megachiropterans, and euprimates or distinguish these taxa from microchiropterans. There is one feature shared by colugos and euprimates, a course for the maxillary artery lateral to Meckel's cartilage and ventrolateral to the lateral pterygoid muscle (CS 12.1), but megachiropterans exhibit the course found in microchiropterans, scandentians, and macroscelideans (CS 12.2). A colugo + euprimate clade, has been supported by a recent analysis of DNA sequence changes (Ammerman and Hillis, 1992), and a maxillary artery running ventrolateral to the lateral pterygoid represents a potential morphological synapomorphy for this grouping. A course for the maxillary artery as in colugos and euprimates has been reported elsewhere only in marsupials and the xenarthran *Tamandua* (Wible, 1987).

No derived features of the cranial circulation support the particular arrangement of taxa in figure 1C and D. Lagomorphs, scandentians, and lemuriform euprimates do share an arterial foramen in the tegmen tympani, but in lagomorphs and ptilocercines the occupant is the ramus superior (CS 7.2) whereas it is the proximal stapedial in the other taxa (CS 7.1). Oddly enough, colugos share the most derived features of the cranial circulation with lagomorphs and with artiodactyls. Shared with lagomorphs is the absence of the proximal stapedial artery (CS 4.1), absence of foramina for the ramus temporalis (CS 8.1), absence of the cranio-orbital foramen (CS 9.1) and sulcus (SC 19.2), a pterygoorbital artery (CS 13.1), and a sinus communicans (CS 18.1). Shared with artiodactyls is the absence of a mastoid foramen (CS 11.1) and an arteria anastomotica (CS 15.1), which also incorporates an intracranial rete mirabile (CS 16.1). However, all of these derived features have a history of convergent appearances in other eutherian groups. The most unusual feature, a pterygoorbital artery, occurs elsewhere only in rodents, i.e., octodontoids, hystricoids, thryonomyoids, and bathyergoids, and some sciuroids and cavioids (Wible, 1984, 1987). But this distribution requires a minimum of two origins within Rodentia when mapped on phylogenies accepted by most authors (Luckett and Hartenberger, 1985)—within Hystriognathi and within Sciuroidea.

Of the various higher-level hypotheses in figure 1, only chiropteran monophyly has received broad support of late from cranial, postcranial, and molecular analyses (Novacek, 1992). Hypotheses of chiropteran diphyly are not dead, but appear to be suffering. Despite the fact that colugos are not linked with bats in recent analyses of DNA sequence changes (e.g., Adkins and Honeycutt, 1991; Bailey et al., 1992; Ammerman and Hillis, 1992), I am inclined, based on cranial and postcranial evidence (Novacek and Wyss, 1986; Wible and Novacek, 1988), to continue my support for this grouping. In fact, my previous support has been strengthened by the discovery here that what I thought was a chiropteran synapomorphy also appears in colugos—a course for the ramus infraorbitalis dorsal to the alisphenoid. The inclusion of colugos and bats within the superorder Archonta along with euprimates and scandentians remains a very weakly supported hypothesis, and I await phylogenetic analyses that incorporate the discovery of new relevant fossils and of new characters in relevant fossils and living forms.

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